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## **EXPLORING THE UNKNOWN IN A WELL-KNOWN SYSTEM**

*Ecology and ecosystem effects of the invasive polychaete  
genus Marenzelleria spp. in the northern Baltic Sea*

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ACADEMIC DISSERTATION

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**Cover illustration:** Laura Kauppi

*When we can't think for ourselves, we can always quote.*

Ludwig Wittgenstein

# ABSTRACT

Introductions of non-native species are changing the composition of plant and animal communities worldwide. Especially in marine systems eradication is most often not possible and it is therefore imperative to know the impact of the non-native species on the surrounding ecosystem. In order to assess the ecological impact of non-native species, basic knowledge of the species' biology, ecology and effects on ecosystem functions in their new environment is needed but often lacking. Naturally low species richness and frequent disturbances occurring in the system make the Baltic Sea one of the most heavily invaded seas in the world. One of the most successful invaders has been the infaunal spionid polychaete genus *Marenzelleria*, three species of which now occur in the Baltic Sea, *M. viridis*, *M. neglecta* and *M. arctia*. Their differing burrowing and ventilation behavior compared to the native species suggest an impact on nutrient cycling e.g. through enhanced burial of phosphorus in reoxygenated sediment. Modeling and experimental studies conducted thus far have, however, produced complex results. Moreover, results from simplified, highly controlled experiments may not be directly applicable in nature considering the spatial and seasonal variation in the abiotic and biotic factors.

In this thesis a combination of monitoring data, field surveys and laboratory experiments were used to investigate the ecosystem effects of *Marenzelleria* spp. Using publicly available benthic monitoring data the invasion history and current distribution of *Marenzelleria* spp. in the Baltic Sea was summarized. It occurs in the entire Baltic Sea with highest densities in deeper (over 30 m) areas. Knowledge of population dynamics of species is essential for predicting their impact and occurrence in the changing environment. An observational study conducted at five different sites along a depth gradient from 5 to 33 m comprising muddy and sandy sites revealed differing population dynamics and productivity of *Marenzelleria* spp. depending on site, depth and species identity. Habitat preferences of the three different species differ with *M. arctia* clearly preferring deeper sites, all three species co-occurring at muddy sites up to 20 m depth, and *M. viridis* and *M. neglecta* occurring together and hybridizing at sandy sites. Monthly population and solute flux measurements revealed that seasonal differences in biotic and abiotic factors lead to variation in the relative importance of *Marenzelleria* spp. on an important ecosystem function,

nutrient cycling. The contribution of *Marenzelleria* spp. to nutrient cycling was highest during spring when food input to the benthos is high. An experimental study demonstrated density-dependent effects of *M. arctica*, *M. neglecta* and *M. viridis* on bioturbation metrics and solute fluxes, implying spatial and temporal variation in their impact on nutrient cycling following changes in their densities and biomass over the year. The impact could be modified by the composition of the surrounding macrofauna community and the variation in abiotic factors. Further, combining the observational and experimental results, implies a possible enhancement of phosphorus binding capacity by *Marenzelleria* spp. in deeper areas especially during summer when oxygen conditions deteriorate and densities increase, but an enhancement of phosphate effluxes in normoxic areas through enhanced remineralization of organic matter. Through density-dependent effects on bioirrigation and directly on ammonium fluxes, the genus also has an impact on nitrogen cycling.

The results from this thesis imply spatial and seasonal differences in the impact of *Marenzelleria* spp. on nutrient cycling related to the environmental conditions and to the densities and biomasses of *Marenzelleria* spp. and other macrofauna. At disturbed sites *Marenzelleria* spp. could possibly enhance phosphorus burial and thus remove nutrients from primary production, whereas at undisturbed, normoxic sites they could enhance organic matter remineralization thus preventing deposition of large quantities of organic matter on the sea floor. The results also highlight the need to study the effects on non-native species in the natural environment incorporating the spatial and seasonal variability, and natural community composition in order to accurately estimate their contribution to ecosystem function. Knowing the basic biology and ecology of the non-native species is important for understanding the consequences of biological invasions.

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# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

- I. Kauppi L., Norkko A., Norkko J. 2015. *Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes Marenzelleria spp. in the Baltic Sea*. Biological Invasions 17(7): 2055-2074.
- II. Kauppi L., Norkko A., Norkko J. 2018. *Seasonal population dynamics of the invasive polychaete genus Marenzelleria spp. in contrasting soft-sediment habitats*. Journal of Sea Research 131: 46-60.
- III. Kauppi L., Norkko J., Ikonen J., Norkko A. 2017. *Seasonal variability in ecosystem functions: quantifying the contribution of invasive species to nutrient cycling in coastal ecosystems*. Marine Ecology Progress Series 572: 193-207.
- IV. Kauppi L., Bernard G., Bastrop R., Norkko A., Norkko J. *Increasing densities of an invasive polychaete enhance bioturbation with variable effects on solute fluxes*. In review.

## Author contributions

	I	II	III	IV
<b>Study design</b>	LK, JN, AN	LK, JN, AN	LK, JN, AN	LK, GB, JN, AN
<b>Sampling</b>	LK	LK, JN	LK, JN	LK, GB
<b>Analyses</b>	LK	LK	LK, JI	LK, GB, RB
<b>Writing</b>	LK, JN, AN	LK, JN, AN	LK, JN, AN	LK, GB, RB, JN, AN

LK = Laura Kauppi, JN = Joanna Norkko, AN = Alf Norkko, JI = Jussi Ikonen, GB = Guillaume Bernard, RB = Ralf Bastrop



# 1 INTRODUCTION

Oceans cover 70 % of the world's surface making the soft-sediment ecosystem the second largest ecosystem in the world after the pelagic realm. Coastal areas are responsible for most of the primary production in marine ecosystems, and are also the most densely inhabited and heavily built-up areas in the world. Therefore, a major part of the coastal ecosystems are under high anthropogenic stress, such as overfishing, habitat degradation and eutrophication, likely disrupting the functioning of these ecosystems, and thus endangering the ecosystem services provided by these systems to humans (Levin et al. 2001, Lotze et al. 2006). Coastal ecosystems are also among the most highly invaded ecosystems in the world due to naturally low species richness in estuarine conditions, combined with anthropogenic stressors and increasing global transport of goods making these systems more vulnerable to species introductions (Cohen & Carlton 1998). Species introductions and invasions are considered as a major threat to the functioning of many both terrestrial and aquatic ecosystems around the world due to the changes non-native species bring about in the structure of both plant and animal communities that can alter ecosystem functioning (Mack et al. 2000, Ehrenfeld 2010, Vilà et al. 2011, Ricciardi et al. 2013). However, the effects of these changes are highly context-dependent (Sellheim et al. 2010, Ricciardi et al. 2013) hence highlighting the importance of examining the ecology and ecosystem effects of non-native species thoroughly before making judgements about whether these effects are negative or positive (Davis et al. 2011). This has important implications for conservation and management of the marine environment.

The Baltic Sea is an anthropogenically stressed, naturally low-diverse, brackish-water system, which makes it vulnerable to species introductions (Leppäkoski et al. 2002). Despite the high number of reported species invasions in the system, the ecology of many invaders remains largely unstudied. This concerns also one of the most successful invaders, the spionid polychaete genus *Marenzelleria*, for which a critical evaluation of effects on the ecosystem is lacking. The aim of this thesis is to summarize the

distribution and ecology of a successful invader in the Baltic Sea, and to explore its impact on ecosystem functioning by quantifying its contribution to nutrient cycling.

## **1.1 BIOLOGICAL INVASIONS IN MARINE ECOSYSTEMS**

The increase in global commerce and aquaculture has increased the amount of marine biological invasions during the past decades (Cohen & Carlton 1998, Bax et al. 2003, Molnar et al. 2008). A major pathway for introductions is global shipping, through which non-native species can be introduced to ecosystems on the other side of the world via the ballast water and hull fouling of the ships. In perhaps the most heavily invaded, and studied, marine system in the world, San Francisco Bay, invasions have had consequences at species-, community- as well as ecosystem-level. These include changes in demography of native species, formation of new habitats with facilitation creating unique communities, and changes in the strength of the benthic-pelagic coupling (summarized e.g. in Grosholz 2002). Like the Baltic Sea, the area around San Francisco Bay is densely inhabited, with a lot of marine traffic increasing the anthropogenic stress to the system (Cohen & Carlton 1998, Williams et al. 2013) in addition to the natural stress to the native communities caused by the highly variable estuarine conditions.

Invasion is the end point of a process with several stages including transport, introduction, establishment and spread, where factors at each stage can prevent the movement to the next stage (Lockwood et al. 2013). These factors can be associated with the characteristics of the abiotic and/or biotic environment and the characteristics of the non-native species themselves (Williamson & Fitter 1996, Mack et al. 2000, Naeem et al. 2000, Sax & Brown 2000, Mata et al. 2013). Taxa with opportunistic life histories, such as many spionid polychaetes, capable of rapidly reproducing and exploiting available resources, are generally successful invaders. Spionidae as a family rank highest of all polychaete taxa in numbers of invasive genera (Çinar 2013). A long pelagic larval phase facilitates their

spread in the ballast water to new areas, and mobility of adults can enhance establishment and spread in the new area.

Invasions are often coupled with disturbances that disrupt the native community structure and leave resources unused (Shea & Chesson 2002, Norkko et al. 2006). Similarly, less diverse communities, either functionally or taxonomically, such as the benthic communities in the Baltic Sea (Leppäkoski et al. 2002, Bonsdorff 2006), might be more susceptible to species invasions due to the low diversity leaving vacant niches in the community (Tilman 2004, Stachowicz & Byrnes 2006).

## **1.2 IMPACTS OF NON-NATIVE SPECIES**

Studies reporting on impacts of invasive species on native ecosystems have often failed to clearly define the terms central to the studies, such as invasive and impact, and used subjective adjectives such as “good” or “bad” depending on how and from which point of view the impact has been defined, calling into question the need for the existence of the entire field of invasion science (Ricciardi et al. 2013, Simberloff et al. 2013, Jeschke et al. 2014). Here, introduction means the human-aided arrival of a species to a new area, either intentional or unintentional, non-native is a species not previously observed in the geographic area, invasive refers to a species/taxon/population undergoing or undergone establishment and subsequent rapid range expansion and population increase. Note that also native species can become invasive but their impact is generally considered to be less dramatic than the non-native species, which may possess traits not previously present in the community (Simberloff et al. 2011, Thomsen et al. 2014). Impact can be defined in different ways depending on if we want to investigate impact from a socio-economic or ecological point of view. Here the meaning of impact is predominantly ecological, i.e. any structural and/or functional change occurring in the native ecosystem due to the arrival of the non-native species (Simberloff et al. 2013, Jeschke et al. 2014).

Once a population of non-native species has established itself, it is, logically, bound to have an impact on the surrounding ecosystem,

but this impact need not to be negative (Sellheim et al. 2010, Norkko et al. 2012). However, surprisingly few quantitative studies on the impact of invasives on ecosystem function exists to this day (Vitousek 1990, Strayer 2012). Changes in community structure, however, have been recorded, such as increased densities and biomasses of benthic species following introduction of the Asian clam *Corbicula fluminea* in Portugal (Novais et al. 2015), and prevention of recovery of the native fauna in the San Francisco Bay estuary by the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990). Changes in function have been assumed based on changes in structure. An increasing number of studies from both terrestrial and aquatic systems report a context-dependency of the invasion process, with highly complex responses and interactions that can act in unpredictable ways (Vilà et al. 2011, Thomsen et al. 2014). For example, a recent meta-analysis (Thomsen et al. 2014) found negative effects of marine invaders on biodiversity within a trophic level, but positive effects on higher trophic levels. As biological invasions are often associated with disturbances in the abiotic environment, it can be difficult to distinguish the driving force of the disturbance from that of the invader as a driver of ecological change in the community (MacDougall & Turkington 2005). Indeed, MacDougall and Turkington (2005) conclude that the invaders often seem to be just “passengers along for the environmental ride”. The traits that non-native species possess play a key role, along with fluctuations in abiotic and biotic factors, in determining invasion success (Mata et al. 2013) but also in determining the effects of the non-native and native species on ecosystem functioning (Hooper et al. 2005, Ehrenfeld 2010).

### **1.3 SOFT-SEDIMENT ECOSYSTEMS**

The structure of animal communities in soft sediments is affected by abiotic drivers, such as physical forces of waves and currents, sediment characteristics, temperature and food supply, as well as by biotic drivers, such as competition for resources and predation (Gray & Elliott 2009). Animal communities in deeper areas below the photic zone depend on the primary production in the water column

for their survival, whereas in situ primary production is possible in shallower areas. A tight benthic-pelagic coupling, where the primary production from the water column sinks down to the sea floor and is remineralized back to nutrients available for use by the primary producers is vitally important for the functioning of the marine ecosystem (Griffiths et al. 2017). Changes in the strength of this coupling, e.g. due to eutrophication leading to excessive amounts of organic matter production, interfere with the functioning. In the case of eutrophication, this results in a build-up of organic matter on the sea floor that the benthic organisms do not have the capacity to process, which can lead to hypoxia/anoxia as oxygen is used up by the degradation processes (Rabalais et al. 2014, Norkko et al. 2015). Water column stratification, either permanent or seasonal, can promote hypoxia formation, especially in deeper areas. Hypoxia, and other disturbances, lead to the replacement of sensitive often long-lived, large animals, by more tolerant, shorter-lived species with opportunistic behaviour (Pearson & Rosenberg 1978), characteristic of many non-native species. The non-native species may possess traits unique to the system, or occur in such high numbers that they could play a significant role in important ecosystem functions, such as nutrient cycling and primary production (Higgins & Vander Zanden 2010, Norkko et al. 2012, Norkko et al. 2015).

Nutrient cycling is an essential function of soft-sediment ecosystems in aquatic environments, as well as of soil ecosystems in terrestrial environments. The organic matter produced by primary producers is ultimately remineralized by microbes in the sediment, but macrofauna also contribute to nutrient cycling by stimulating the microbial processes (Mermillod-Blondin et al. 2004, Foshtomi et al. 2015), and by their bioturbation (Kristensen et al. 2011b). Bioturbation is defined as the sediment reworking and burrow ventilation by fauna in the sediment (Kristensen et al. 2011b). These activities change the chemical gradients in the sediment porewater, thus affecting the diffusion of substances to and from the porewater and through the sediment-water -interface (Mortimer et al. 1999, Mermillod-Blondin & Rosenberg 2006). The burrowing and flushing of the burrows also affect oxygen penetration into the sediment thus influencing the degree to which aerobic vs. anaerobic respiration

processes are responsible for nutrient remineralization (Vopel et al. 2003). Macrofauna also directly contribute to sediment oxygen consumption through their own respiration and to nutrient dynamics through their excretion (Vanni 2002). Macrofauna activities, such as sediment mixing and burrow ventilation, are thus a key component in benthic-pelagic coupling.

Infaunal polychaetes affect biogeochemistry and thus the exchange of solutes at the sediment-water interface through their particle reworking and burrow ventilation activities, hence their key role in nutrient cycling (Kristensen et al. 2011b). The effect of this is modified by community structure, density, biomass, and abiotic factors, such as sediment type (Mermillod-Blondin et al. 2005, Braeckman et al. 2014, Queirós et al. 2015). The invasive polychaete genus *Marenzelleria* spp. investigated in this thesis differs from the native Baltic Sea fauna by their bioturbation-related traits: they burrow deeper than the native fauna and build branching burrows thus affecting the redox conditions of the sediment with potentially large influence on nutrient cycling (Renz & Forster 2013, 2014). Several experimental studies on the effects of *Marenzelleria* spp. on nutrient cycling and on its interactions with other species have produced complex results depending e.g. on the species and sediment type used (Hietanen et al. 2007, Kristensen et al. 2011a, Quintana et al. 2011). Due to the experimentally demonstrated higher tolerance for low oxygen conditions compared to the native fauna (Schiedek 1997b, a), *Marenzelleria* spp. have been suggested to be able to act as ecosystem engineers, by colonizing areas suffering from hypoxia, reoxygenating the sediment and thus facilitating the return of the native fauna. Reoxygenation of the sediment could also lead to enhanced binding of phosphorus with iron oxyhydroxides, which would mitigate eutrophication in the long term (Hietanen et al. 2007, Norkko et al. 2012). The activities of *Marenzelleria* spp. can also lead to enhanced burial of organic matter thus slowing down the oxygen-consuming remineralization processes (Josefson et al. 2012). Single-species experiments and modelling studies provide important mechanistic understanding, but species rarely occur alone in nature. Moreover, experiments are limited in space and time and results may therefore not be directly applicable in nature in an environment with

large seasonal variability in abiotic and biotic conditions possibly modifying the effect of the biota (Snelgrove et al. 2014, Lohrer et al. 2015).

#### **1.4 BIODIVERSITY-ECOSYSTEM FUNCTIONING (BEF) RELATIONSHIPS**

Loss of biodiversity has been found to impair ecosystem function in many studies (Worm et al. 2006, Hooper et al. 2012), but the actual effect in real-world ecosystems depends on multiple drivers such as climate and anthropogenic disturbances (Eisenhauer et al. 2016). Additionally, the effects of biodiversity and environmental factors, respectively, in driving ecosystem processes need to be explored further to understand the relative importance of these for ecosystem functioning (Villnäs et al. 2012, Braeckman et al. 2014, Queirós et al. 2015). Biological invasions, feared to cause extinctions of native species, rather often result in a gain of species instead, but the effect of species gain on ecosystems is poorly studied (Gurevitch & Padilla 2004, Stachowicz & Byrnes 2006, Gamfeldt et al. 2015, Hewitt et al. 2016). Whether species are lost or gained, the focus should be on their respective functional traits and their interaction with other biota and the environment in defining their effect on ecosystem functioning (Wardle et al. 2011, Kristensen et al. 2014).

Due to the inherent variability of nature in both space and time, the scale at which studies are conducted can affect their outcome. The difference in spatial and temporal scale between experiments and reality has led to differential interpretation of the effect of biodiversity on invasion resistance of communities resulting in a phenomenon called the “paradox of invasion”, where experimental results suggest that increasing biodiversity increases the invasion resistance of communities, whereas observational studies indicate that more species-rich communities actually house a proportionally larger number of non-native species (Sax & Brown 2000, Stachowicz & Byrnes 2006, Fridley et al. 2007). Scale of study can also affect the conclusions drawn about the impacts of biodiversity to ecosystem functioning (Snelgrove et al. 2014, Lohrer et al. 2015), with short-term experiments generally concluding an enhancement of

ecosystem functions by increasing biodiversity, which might be obscured in longer-term studies due to fluctuations in the environmental conditions (Godbold & Solan 2009). Seasonal changes in abiotic conditions are prominent in ecosystems at temperate and high latitudes, with marked changes in, for example, temperature and organic matter input to the sea floor. Seasonal variation in the biotic factors, species densities and biomasses, can affect BEF relationships as dominance relationships, and interaction strengths change with season (Chapin et al. 1997, Cardinale et al. 2000, Karlson et al. 2016). Scale is also of fundamental importance when assessing the impact of non-native species on the surrounding ecosystem (Gravel et al. 2016), because the impact might change over time (e.g. between the lag phase in densities and invasion, cf. Hobbs et al. 2009, Ricciardi et al. 2013).

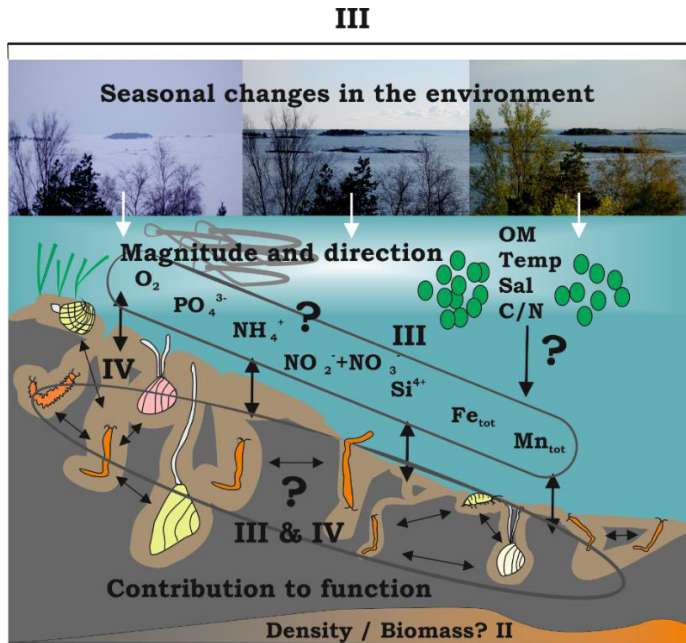


## 2 AIMS OF THE THESIS

This thesis aims at investigating the ecology and ecosystem effects of the invasion by the spionid polychaete genus *Marenzelleria* spp., and in particular on a key ecosystem function, nutrient cycling, in the northern Baltic Sea. The genus was observed for the first time in the southern Baltic Sea in 1985 (Bick & Burckhardt 1989), and reached the southern Finnish coast in 1990 (Norkko et al. 1993, Stigzelius et al. 1997). The presence of in total three species of the genus has now been confirmed in the Baltic Sea: *M. viridis* (Verrill, 1873) and *M. neglecta* Sikorski and Bick, 2006 of North American origin (George 1966), and *M. arctica* of Arctic origin (Blank et al. 2008). 2008). The most probable means of introduction into the Baltic Sea for all species is in the ballast water of ships (Bastrop et al. 1998). Reliable identification of the species is only possible with genetic analyses. *Marenzelleria* are mobile, burrow-dwelling sub-surface deposit-feeders. *M. viridis* and *M. neglecta* burrow deep into the sediment (20-25 cm), and are also generally larger than *M. arctica* (burrow to 10 cm) suggesting differences in their effects on bioturbation and nutrient cycling.

This thesis also investigates the distribution, population dynamics, and production of *Marenzelleria* spp. in the Baltic Sea (Fig. 1). Despite a number of studies on the impact of *Marenzelleria* spp. on its surrounding ecosystem, the distribution of the genus in the Baltic Sea, habitat preferences and population dynamics of the three different species are largely unknown (Papers I and II). Population dynamics have fundamental effects on species interactions and ecosystem functioning. As the variation in the environmental conditions can cause variation in the contribution of macrofauna to ecosystem functions, the importance of this variability for the role of *Marenzelleria* spp. along with other factors in seasonal nutrient dynamics was investigated (Paper III). Studies quantifying the effects of invasive species and the seasonal importance of abiotic vs biotic drivers on ecosystem functioning are rare. This information is however crucial for modelling, management and conservation purposes. The density-dependent effects of *Marenzelleria* spp. on nutrient cycling were studied experimentally

(Paper IV) within the naturally occurring animal community. Hence the general aim of this thesis is filling gaps in our knowledge about the relative importance of abiotic vs biotic drivers for ecosystem functioning in seasonally fluctuating environments, as well as on the importance of non-native species and species gain on ecosystem functions and processes embedded in this variability in the abiotic and biotic environment (Wardle et al. 2011, Perkins et al. 2015, Eisenhauer et al. 2016). Moreover this thesis provides insights into the density-dependence of invasive species and BEF-relationships. By combining experimental and observational evidence of the whole community and environmental variables, this thesis aims at providing a more realistic assessment of the effects of *Marenzelleria* spp. on the real-world Baltic Sea ecosystem (Snelgrove et al. 2014, Lohrer et al. 2015).



**Figure 1.** Illustration of a simplified Baltic Sea ecosystem showing the benthic compartment with macrofauna and the pelagic compartment with primary producers and consumers (e.g. fish) depicting the knowledge gaps targeted in the different original research Papers of this thesis: How are seasonal changes in the abiotic environment translated into changes in the populations of native and non-native species, and how will these changes affect the importance of different drivers of nutrient cycling (II-III)? Are the effects of the invader on the functions and processes density-dependent (VI)?

## **3 METHODS**

### **3.1 STUDY AREAS**

The study area covered the whole Baltic Sea inside the Danish Straits but focused specifically the Finnish coast of Gulf of Finland (I), five macrofauna sampling locations in the proximity of Tvärminne Zoological Station in southern Finland (59°50.896', 23°15.092') (II), two of which were also used for nutrient flux measurements (III). The experiment was conducted in the laboratory facilities at Tvärminne Zoological Station (IV). The benthic monitoring data collected at Tvärminne since 1926 was invaluable for this thesis.

### **3.2 THE BALTIC SEA**

The Baltic Sea is a brackish water basin with a total area of 418690 km<sup>2</sup> and a maximum depth of 459 m. A prominent feature of the Baltic Sea, being situated in the temperate zone, is the seasonality in the abiotic environment. The Baltic Sea is characterized by steep horizontal, vertical and seasonal gradients in hydrography that are either permanent, such as the halocline occurring in 50-60 m depth, or seasonal, such as the thermocline forming during summer, when the surface water warms, or during winter when it cools down. This causes the surface and bottom water to have different densities and leads to a stratification of the water column. The thermocline is disrupted during spring and fall, when the surface and bottom water reach the same temperature, and the entire water column undergoes a circulation down to the halocline. Stratification reduces mixing of the water column, which during intense degradation of organic matter settling on the sea floor can lead to hypoxia and/or anoxia, both common in the deep parts of the Baltic Sea. Horizontally, decreasing salinity towards the north and east, as well as from the outer to the inner archipelago limits the distribution of marine species and of freshwater species in the opposite direction (Bonsdorff 2006, Villnäs & Norkko 2011). The naturally low species richness and the frequent disturbances occurring in the system make the Baltic Sea very vulnerable to species introductions, and it has therefore been called “a sea of invaders” (Leppäkoski et al. 2002).

### **3.3 DISTRIBUTION AND DYNAMICS OF *MARENZELLERIA* SPP.**

Monitoring data collected around the Baltic Sea allow the study of broad-scale patterns in the benthic communities and were used in Paper I to study the invasion of *Marenzelleria* spp. into the Baltic Sea. The invasion dynamics over time, current distribution and densities were summarized using monitoring data from different sources covering 1790 soft benthos monitoring sites differing in depth from 0 to over 100 m in the Baltic Sea area from inner archipelago to the open sea. The longest time-series was used to study dynamics in species densities, dominance patterns and number of taxa prior to and after the introduction. All together data over several years from 715 benthic and 106 hydrography monitoring sites at the Finnish Coast of the Gulf of Finland were used for analysing the environmental factors associated with the highest densities of *Marenzelleria* spp. on a larger spatial scale.

On a smaller spatial scale but with a near-monthly temporal resolution, the seasonal population dynamics and production of *Marenzelleria arctica*, *M. viridis* and *M. neglecta* were studied at five locations (I to V) with differing depths and sediment type over a year (April 2013 to June 2014) in Paper II. The contribution of biotic (possible intra- and interspecific interactions) and abiotic (sediment characteristics and hydrography) factors to the observed dynamics were also investigated. Studying the population biology of invasive species is important for understanding invasiveness and potential impacts of non-native species, as well as for management purposes. Despite the Baltic Sea being well studied, seasonal population dynamics of *Marenzelleria* spp. have hardly been studied.

### **3.4 THE ROLE OF *MARENZELLERIA* SPP. IN NUTRIENT CYCLING**

Especially in deeper areas, *Marenzelleria* spp. has added functional diversity to the communities (Hewitt et al. 2016) and could therefore have an impact on nutrient cycling. The contribution of macrofauna

including *Marenzelleria* spp. to nutrient cycling in the Baltic Sea has been studied over a range of spatial scales and along disturbance gradients in a limited period of time (Norkko et al. 2015, Gammal et al. 2017), but the seasonal variation has not been explored. Such data are, however, essential especially for modelling purposes in order to more accurately estimate nutrient budgets and target management actions. In Paper III, the seasonal nutrient fluxes, and the effects of *Marenzelleria* spp. and other macrofauna, and different environmental factors (sediment characteristics and hydrography) on nutrient cycling were studied at two sites with contrasting depth, macrofauna community composition, and species identity and population dynamics of *Marenzelleria* spp. Nutrient fluxes were studied in dark incubations of intact sediment cores at in situ temperature onboard r/v Saduria monthly from June 2013 to June 2014.

A combination of experimental and observational studies can give a more realistic understanding of the effects of the different factors on nutrient cycling. A previous modelling study demonstrated that density-dependence could be a key factor affecting the impact of invasive species on ecosystem function (Norkko et al. 2012) but is rarely considered in experimental manipulations. In Paper IV the density-dependent effects of the three different species of *Marenzelleria* spp. on nutrient cycling and bioturbation were studied in a laboratory experiment. Because species rarely occur in isolation, and their impact might be modified by the other taxa present in the community, the density-dependent effects were tested using undisturbed sediment cores containing the natural animal community by adding *Marenzelleria* spp. in five different density treatments (3, 6, 12, 24 or 48 worms added and a control with no added worms). The experimental cores and worms were collected at the vicinity of Tvärminne Zoological Station on one of the sites used for Paper II. In the cores, the density-dependence of sediment reworking, bioirrigation activities and solute fluxes was studied. Solute fluxes were measured using similar dark incubations as in Paper III.

### 3.5 DATA ANALYSES

Due to the observational nature of the data in the different studies, the statistical methods used were limited to correlational analyses. However, combining knowledge from the observational studies and the mechanistic understanding gained from the experiment in Paper IV (although not highly controlled), along with knowledge of the environment, these results are more readily transferrable to natural ecosystems.

Due to the variability and lack of replication in the monitoring methodology, the distribution and abundance patterns of *Marenzelleria* spp. were studied descriptively. The association of the *Marenzelleria* spp. densities with the environmental factors were investigated using a regression tree -method (Therneau et al. 2010), which is fairly robust for variation in the methodology of the studies (Speybroeck 2012).

The production, elimination and productivity (P/B and E/B ratios) of the populations were studied using the Increment Summation Method (ISM). Pearson product moment correlations were used to investigate the association between the environmental factors and the changes in the population densities, and the possible effects of intra- and interspecific competition on individual growth. Population growth rates were investigated by assessing the Von Bertalanffy growth rates according to Brey (2001).

In Papers III and IV, multivariate variation partitioning techniques (distance-based linear modeling, DistLM (III) combined with distance-based redundancy analysis, dbRDA (IV)) were used to investigate the effects of the different predictor variables on the response variables, which in this case were a Euclidean distance matrix of the combined solute flux (III), or a Euclidean distance matrix of individual solute fluxes (III and IV). The dbRDA analysis was used to visualize the relationship between the selected predictor variables and the different solute fluxes in the multivariate space (III and IV). All analyses were performed with PRIMER 6 and with its PERMANOVA+ add-on (Anderson et al. 2008).

## 4 MAIN FINDINGS OF THE THESIS

The invasive spionid polychaete genus *Marenzelleria* spp. is one of the most successful non-native taxa in the Baltic Sea and is suspected to have profound but complex impacts on ecosystem functionality. The summary of its distribution (Paper I; Fig. 2 this thesis) 25 years after introduction to the southern Baltic Sea revealed that the genus has spread to the entire Baltic Sea, where it at times has become a dominant element of the benthic fauna. The highest abundances were observed in the deeper bottoms (over 30 m but less than 60 m) and in the outer archipelago. The occurrence of in total three species of the genus has now been confirmed also in the northern Baltic Sea (Paper II), and they can cohabit muddy sites up to 20 m depth. At the deeper site, only *M. arctica* was observed, whereas the shallow, sandy site was inhabited by *M. viridis* and *M. neglecta*, which also hybridized at this site (Paper IV; Bastrop et al. unpublished data). The species showed differing population dynamics, with the North American species, *M. viridis* and *M. neglecta*, practically disappearing during the winter, but with very high abundances and secondary production during the peak reproduction season in spring. In contrast, the Arctic species, *M. arctica*, generally had lower abundances and biomass production, but a more stable presence throughout the year at the deeper site (Paper II). The biomass production was highest at the 20 m deep site III, where all three species recruit (Paper II). The species complex is numerically dominant in these benthic communities, along with *M. balthica*.

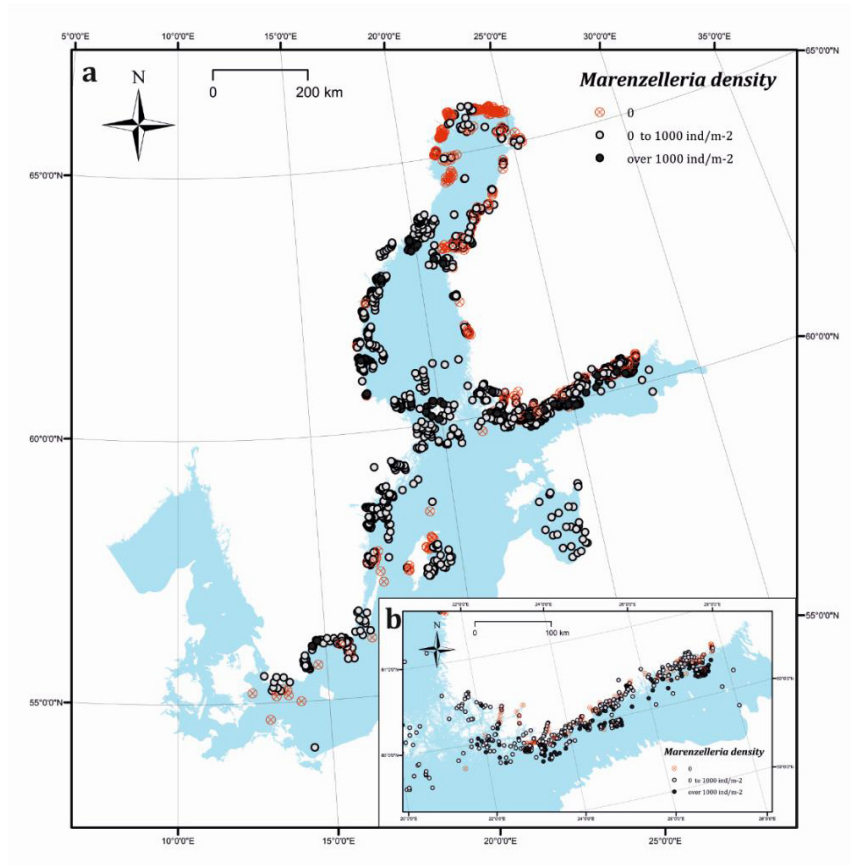
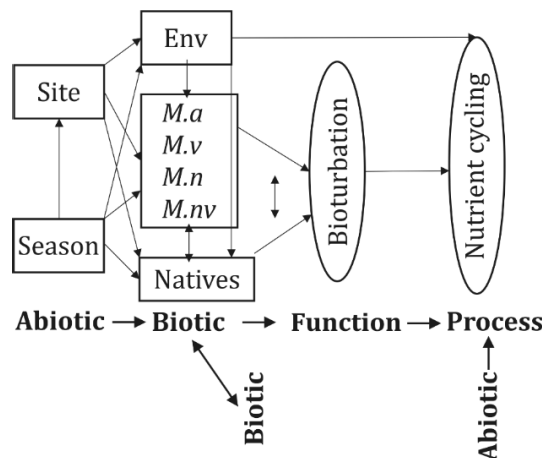


Figure 2. Maps showing the summarized distribution and densities of *Marenzelleria* spp. in the Baltic Sea (a) and especially at the Finnish coast of the Gulf of Finland (b). The sites with over 1000 ind  $m^{-2}$  in (b) are generally found at over 30 m depth according to the regression tree analysis. The species identity of *Marenzelleria* spp. at these sites is most likely *M. arctica* (Paper II; Bastrop et al. unpublished data). Figure modified from Paper I.

Seasonal variation was apparent in the ecosystem processes with changes in both magnitude and direction of the solute fluxes, and these were driven by seasonal changes in the abiotic (mostly temperature and organic matter quantity and quality) and biotic (changes in the macrofauna densities) variables (Fig. 3). The contribution of *Marenzelleria* spp. to nutrient cycling varied seasonally with largest effect at both shallow and deep sites during spring, when organic matter input is highest (Heiskanen & Tallberg 1999). Adding complexity, *M. neglecta* and *M. viridis*, and of *M. arctica* had variable effects on the different bioturbation parameters,



which resulted in variable contributions to the fluxes of individual nutrients (Paper IV). This could also be seen in their seasonally and spatially variable effects on these fluxes in nature (Paper III). Generally the role of *Marenzelleria* seems to be more prominent in nitrogen cycling than in phosphorus cycling in normoxic environments. However, possible interactions with the native macrofauna, and the abiotic environment also affect the outcome of the *Marenzelleria* bioturbation: the presence of other species can modify the effect, and seasonal changes in the environment, e.g. hypoxia, can change the direction of the effect of *Marenzelleria* bioturbation on phosphate fluxes. On the shallow sites where they co-occur, the interactions with the native biota, i.e. predation by *Hediste diversicolor*, may have direct effects on the presence, survival and population dynamics of *Marenzelleria*.



**Figure 3.** Conceptual figure modified from Paper IV illustrating the effects of abiotic and biotic variables for bioturbation and nutrient cycling. Seasonal changes in the environment affect nutrient cycling both directly and indirectly through the impact on macrofauna communities and these effects are site-dependent. Interactions with the environment and the native members of the macrofauna community modify the outcome of the impact of the invasive *Marenzelleria* spp. on bioturbation and nutrient cycling. Biotic factors interact with each other modifying the effect on function. Abiotic factors can affect the process, in this case nutrient cycling, also directly through e.g. changes in temperature and oxygen conditions. The one-sided arrows illustrate an effect, the double-sided arrows an interaction. Env=environmental variables (bottom-water temperature, salinity, pH, oxygen content, sediment organic matter content and C/N ratio), M.a=*M. arctica*, M.v=*M. viridis*, M.n=*M. neglecta*, M.nv=hybrids of *M. neglecta* and *M. viridis*.

## 5 RESULTS AND DISCUSSION

### 5.1 SPATIAL AND TEMPORAL DISTRIBUTION OF MARENZELLERIA SPP. IN THE BALTIC SEA

The first comprehensive summary of the distribution of *Marenzelleria* spp. in the Baltic Sea based on monitoring data (Paper I) revealed the spread of the species complex to the entire Baltic Sea, and its dominance in many areas, justifying further study of these species. Disturbance in the form of eutrophication coupled with an increase in hypoxic areas in the Baltic Sea has led to the impoverishment of the benthic communities in the Baltic Sea (Villnäs & Norkko 2011). In combination with the naturally low species richness, this has made the system more vulnerable to species introductions (Leppäkoski et al. 2002, Bonsdorff 2006). Natives may not be adapted to changes in the environmental conditions, making them inferior competitors (Sax & Brown 2000). Increasing temperatures in the northern Baltic Sea changed the structure and dominance patterns of native communities (Rousi et al. 2013) even before the first observations of *Marenzelleria* spp. (Paper I, Fig. 3; Hewitt et al. 2016). Due to niche partitioning, the polychaetes use resources in a partly different way from the native species in the system (Karlson et al. 2011). This makes resource use more efficient and reduces competition for resources, which could have contributed to the invasion success of *Marenzelleria*. However, changes in the dominance of the key species in the community before the establishment of *Marenzelleria* were ultimately caused by changes in the abiotic environment unfavourable for the native amphipod, *Monoporeia affinis*, species, which led to changes in the structure of the biotic community (Rousi et al. 2013), an example of the abiotic and biotic drivers acting together to allow a successful invasion (Gurevitch & Padilla 2004, Hobbs et al. 2009). That *M. neglecta* and *viridis* at the shallower sites recruits before the key species *M. balthica* (Paper II) might have facilitated their establishment, but clearly has not been competitively limiting for *M. balthica*. Renewed recruitment of *M. affinis*, however, also coincided with that of *M. arctica*, which might prevent the dominance of *M. affinis* even if environmental conditions improve in the future. Regardless of the

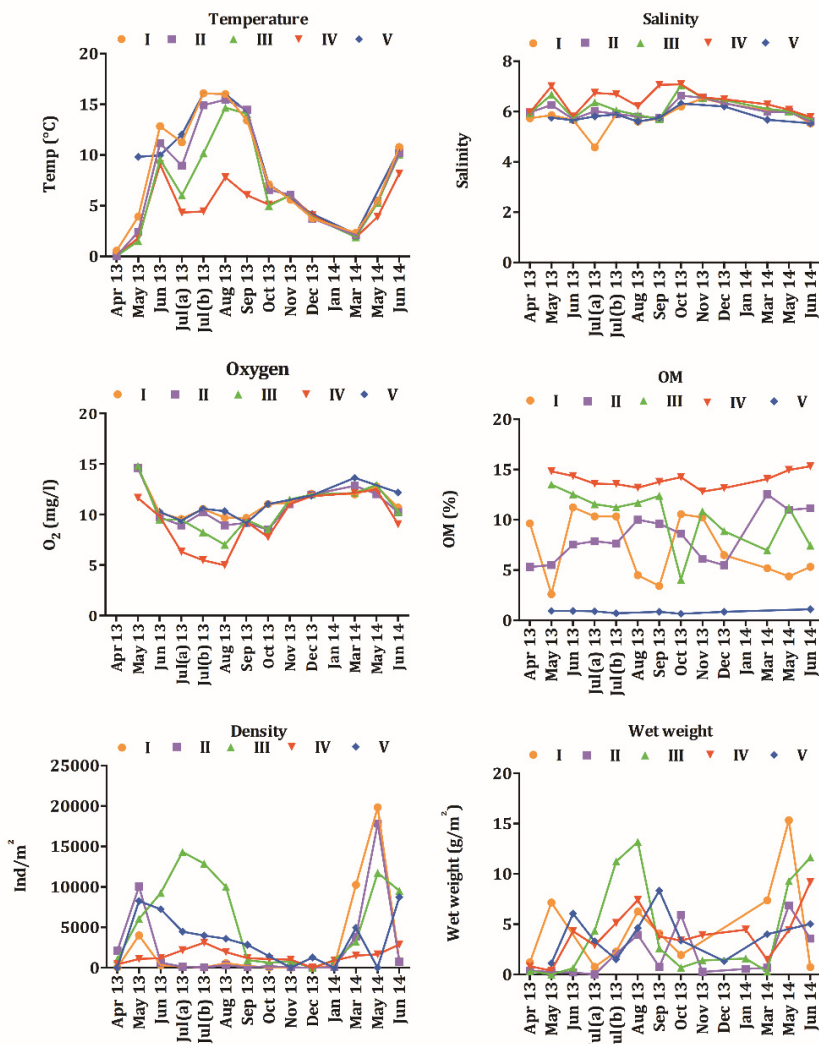
cause of the invasion, the three *Marenzelleria* spp. are in the Baltic Sea to stay and are bound to interact with the native community and the environment, and thus have an impact on the functioning of the system. From a conservation and management point of view it is important to know the relative importance of different factors in driving the functions in order to target the actions (Hobbs & Huenneke 1992, Hobbs et al. 2009).

A closer look at the coastal zone of the Gulf of Finland on a smaller spatial scale revealed a clear pattern in the densities of *Marenzelleria* spp. along a gradient from shallower to deeper, and inner to outer archipelago, with highest densities occurring at approximately 20 to 30 m deep sites in the outer archipelago (Paper I). The three species seem to have slightly differing habitat preferences with *M. neglecta* and *M. viridis* preferring sandy and muddy sites up to 20 m depth, and *M. arctica* found only on muddy sites at depths ranging from 5 to 60 m (Paper II, Kauppi et al. unpublished data) thus suggesting that the sites with the highest densities of *Marenzelleria* spp. are the ones where all three species co-occur, or deeper sites with the presence of *M. arctica* only. Even though *Marenzelleria* is reported to be more tolerant to hypoxia than native species (Schiedek 1997 a, b) and can thrive in moderate hypoxia above the halocline in open sea areas of the northern Baltic Sea (Norkko et al. 2015), their densities dropped at depths below 60 m and pH under 7.5 (Paper I, Fig. 4), indicating that despite their higher tolerance to low oxygen concentrations in laboratory studies, their densities also in areas affected by hypoxia are not very high. The differences in species identities at different sites with variable population dynamics (Paper II), and the density- and seasonal dependence of the effects of *Marenzelleria* spp. on solute fluxes (Paper III, IV) implies therefore also spatial differences in their impact on ecosystem functioning.

## **5.2 SEASONAL DYNAMICS IN THE POPULATIONS**

In addition to spatial differences in the average densities on a Baltic-wide scale, the population dynamics and average densities varied seasonally (Paper II, Fig. 4 this thesis) implying also seasonally changing contributions to ecosystem function. *Marenzelleria* spp. practically disappeared for the winter from the muddy sites above 20

m depth. The period during which the polychaetes were present or even numerically dominant was thus very short making their contribution to the community trait composition seasonally variable. At the deeper site, where only *M. arctia* occurs, its population was more stable and the late summer recruitment peak was much smaller. Similarly at the sandy site, with *M. neglecta* and *M. viridis* co-occurring, their presence was more stable and the peaks more moderate. Seasonally, *Marenzelleria* was the numerically dominant taxon only during the recruitment peaks, and then only at the sites down to 20 m depth. The 20 m deep, muddy site could have an important effect on the ecosystem by functioning as a recruitment site for all three *Marenzelleria* species. The site could therefore impact the community assembly processes in adjacent areas. Results of de Moura Queirós et al. (2011) and Karlson et al. (2016) further suggest that local species composition, species identity, density and body size affects ecosystem functioning implying that the recruitment site could affect production and functioning of nearby sites by contributing to changes in community composition. The increased taxa and functional richness at sites XXVI and XLIV (Paper I), but increased taxa turnover at XXVI and decreased trait turnover at XLIV following the arrival and establishment of *Marenzelleria* spp. found by Hewitt et al. (2016) also suggests differences in the invader effects based on the community dynamics of the particular site.



**Figure 4.** Seasonal dynamics in the abiotic (a-d) and biotic (e-f) factors at the site I to V in Paper II, and III. Graphs a to d illustrate variation in the abiotic factors at sites, and graphs e & f variation in abundance and biomass at sites I to V (Paper II and III). Pattern and magnitude for abiotic conditions differs mainly for organic matter. In abundance, Storfjärden (IV) and Brännskär (V) have on average lower and more stable abundance than the other sites, whereas site III differs from the rest with a lot higher summer abundance.

Secondary production provided by healthy benthic communities supports food webs that provide important ecosystem services, such as fisheries, to humans. Effective use of primary production for secondary production also hinders excessive deposition of organic

matter on the sea floor, which eventually may lead to hypoxia due to the slow, oxygen-consuming degradation processes (Conley et al. 2009, Josefson et al. 2012). *Marenzelleria* spp. has been shown to be capable of utilizing organic matter with a different isotopic ratio than the native species (Karlson et al. 2015), indicating that they could have enhanced the organic matter consumption. They also increased the burial of organic matter into the sediment thus potentially slowing down its degradation (Josefson et al. 2012). In Paper II a negative correlation with the organic content of the sediment and the *Marenzelleria* densities at the organic-poor, sandy site suggesting that at these sites they could decrease the amount of organic matter directly transferred to oxygen-demanding remineralization processes (Paper II). Post-invasion values for sediment organic content at the study sites II and IV (Paper II, III) also do not show as clear peaks following peaks in primary production as prior to the invasion (Jäntti et al. 2011), further suggesting more effective use of organic matter. Biomass production of the *Marenzelleria* population (Table 6 in Paper II) was highest at the muddy site III, where all three species recruit and co-occur. The lowest biomass production was exhibited by the *M. arctia* population at site IV. The production also reflects the mean biomasses of the population at these sites. The highest turnover in the population was observed at site III, and the shallow, muddy site I also exhibited a high turnover rate (P/B ratios 8.9 and 7.3 for sites III and I, respectively). Typical of species with opportunistic life histories, spring cohorts had the highest biomass production and growth rates (Zajac 1991a, b). Mean annual production found for spionids generally ranges from 0.08 to 8.06 g AFDW m<sup>-2</sup> per year (Ambrogi 1990, Souza & Borzone 2000) indicating that *Marenzelleria* has a quite high production at all study sites.

### **5.3 MARENZELLERIA SPP. AND ECOSYSTEM FUNCTIONING**

A biological invasion, whether or not accompanied by a loss of native species, is can change the functioning of an ecosystem by altering its trait composition (Wardle et al. 2011, Gamfeldt et al. 2015). Non-native species that differ from the native fauna in their functional

trait composition are thought to affect ecosystem functioning more than invaders with traits similar to those already present in the community (Simberloff et al. 2013). Therefore invasions by native species are considered to have less dramatic consequences, although non-native species invading an empty niche could potentially also have minor effects on ecosystem functioning despite them being functionally different (Hewitt et al. 2016). *M. neglecta*, *M. viridis* and *M. arctia* differ from the native community in their burrowing behavior, by burrowing deeper and building branching burrows, that are flushed periodically (Renz & Forster 2013). They also differ from each other in that *M. viridis* and *M. neglecta* are bigger and burrow deeper (20-25 cm) than *M. arctia* (10 cm) (Renz & Forster 2013).

#### **5.4 CONTRIBUTION TO BIOTURBATION AND NUTRIENT CYCLING**

Bioturbation is an important ecosystem function in soft sediments as well as in soils. In both ecosystems it is a prerequisite for efficient nutrient cycling by providing the starting material for primary production. In terrestrial systems earthworms perform similar functions as polychaetes in the sediment. Invasion of non-native earthworms in northern temperate forests has led to site- and species-specific changes in nutrient cycling and pools in the soil, and in the distribution and function of roots and microbes (Bohlen et al. 2004). In addition to bioturbation, nutrient cycling in marine sediment depends on a number of factors, e.g. temperature, oxygen conditions and organic matter availability. Ultimately the degradation process is carried out by the microbial community, the activity of which can be affected by macrofauna (Braeckman et al. 2010, Foshtomi et al. 2015). Through enhancement of bioturbation in especially deeper, hypoxic areas, *Marenzelleria* spp. could reoxygenate the sediment, leading to an enhanced binding of phosphorus and thus mitigation of eutrophication (Norkko et al. 2012). Jäntti et al. (2011) also suggested a role for *Marenzelleria* spp. in nitrogen cycling by possibly enhancing the nitrification process.

The experimental results by Renz & Forster (2013) indicate a greater effect of *M. neglecta* and *M. viridis* than of *M. arctia* on bioturbation and nutrient cycling. In laboratory conditions, all three

species had very low particle reworking rates, and differed in their effect on solute transport, which in *M. arctia* was more diffusive compared to the nonlocal, advective mode of transport for *M. neglecta* and *viridis* (Renz & Forster 2013). Due to these differences, *M. neglecta* and *M. viridis* could enhance effluxes of ammonium and phosphate and the uptake of oxygen more than *M. arctia* similarly in laboratory conditions (Renz & Forster 2014). These experiments provide excellent mechanistic understanding of the three species alone, but species seldom occur alone in nature. Species interactions might modify the outcome of e.g. biogeochemical processes, and a gain/loss of species might modify species interactions (Mermillod-Blondin et al. 2004, Michaud et al. 2005, Ciutat et al. 2007, Eisenhauer et al. 2016).

Table 1 summarizes the results from the variation partitioning analyses in papers III and IV. The observational data (Paper III) gives insight into the relative importance of different abiotic and biotic drivers over the year, whereas the results of the experiment (Paper IV) demonstrate the relative importance of drivers associated with the biota, such as density, biomass and species identity on nutrient cycling. Different bioturbation parameters were of importance for each nutrient in question, which caused differences in the effect of the three *Marenzelleria* and other species on the different solutes. Fluxes of inorganic nitrogen behaved similarly, and were affected by *Marenzelleria* spp. both directly (the positive effect of *M. arctia* on ammonium fluxes), and indirectly (effects on  $\text{NO}_x$  fluxes) through bioirrigation. On the other hand, phosphate and silicate responded to the same faunal parameters with *M. neglecta+viridis* density predicting variation for both. Since there are spatial and temporal differences in the species distributions and population dynamics, this implies both spatial and temporal differences in their impact on nutrient cycling.

In the presence of the natural community we were able to demonstrate an enhancement of all bioturbation parameters tested (biodiffusion coefficient  $D_b^N$ , maximum penetration depth MPD, percentage of surface reworked SR, and bioirrigation BI) by *Marenzelleria* spp. as a species complex (Paper IV; Table 1c this thesis). There were, however, differences in the effects related to the



species identity: the density of *M. arctia* significantly affected bioirrigation, whereas the density of *M. neglecta* and *M. viridis* had an effect on surface reworking but this was not statistically significant (Paper IV; Table 1c this thesis). Importantly, the outcome of these functions on nutrient cycling seemed to be dependent on the other species and the functions they performed (Michaud et al. 2005, Waldbusser & Marinelli 2006, Ciutat et al. 2007, de Moura Queirós et al. 2011). Waldbusser et al. (2004) found that multispecies assemblages showed lower fluxes than single-species assemblages partly due to interactions between species and species-specific feeding and burrowing behaviour. This highlights the importance of studying the impacts of non-native species embedded in the native community, as in single-species experiments their role could be overestimated.

In general the presence of large clams seems to override the effect of other species; body size has been found to be an important trait for ecosystem functioning also in other studies (Villnäs et al. 2012, Norkko et al. 2013). The native polychaete species *Hediste diversicolor*, on the other hand, readily consumed *Marenzelleria* spp. in the experiment, which could have indirect effects on bioturbation potential through changes in densities due to predation, which was suggested as a potential reason for the decline in *M. viridis* population for the winter in its native range (Sarda et al. 1995). *M. neglecta* and *M. viridis* enhanced the release of solutes more compared to *H. diversicolor* because of differences in their burrow structure and species-specific ventilation behaviour and bioirrigation (Hedman et al. 2011, Kristensen et al. 2011a, Vasquez-Cardenas et al. 2016) thus the predation of *M. neglecta* by *H. diversicolor* can affect the magnitude of solute release.

**Table 1.** Results from the DistLM analyses from the observational study (Paper III) and the experiment (Paper IV) examining (a) the effects of macrofauna and environmental variables on fluxes of individual solutes and on the combined flux of all solutes during different seasons, (b) the effects of macrofauna and bioturbation on solute fluxes and (c) the effects of macrofauna on bioturbation parameters. BT param=bioturbation parameters. High=period of high oxygen consumption, and Low=period of low oxygen consumption used in Paper III to divide the year into two seasons based on the activity of macrofauna and microbial processes that oxygen consumption can be used as a proxy for (Glud 2003). OM=sediment organic matter content, Others=density of other macrofauna than *Marenzelleria*, MPD=maximum penetration depth, SR=percentage of surface reworked,  $D_b^N$ =biodiffusion coefficient, BI=bioirrigation. Bold indicates a statistically significant predictor at the  $\alpha \leq 0.10$  level. AIC=Akaike Information Criterion, Prop.=proportion of variance explained by the predictor, Cum-R<sup>2</sup>=cumulative percentage of variance explained, Corr.=correlation with the dbRDA-axis. Table combined from Papers III and IV.

a) Site	Time	Response	Selected predictors	AIC	Pseudo-F	P	Prop.	Cum-R <sup>2</sup>	Corr.
II (10m)	Year	NO <sub>x</sub>	<b><i>Marenzelleria</i> density</b>	<b>343.59</b>	<b>18.10</b>	<b>0.001</b>	<b>0.26</b>	<b>0.26</b>	-
			<b>Temp</b>	<b>339.8</b>	<b>5.77</b>	<b>0.015</b>	<b>0.08</b>	<b>0.33</b>	+
			<b>Salinity</b>	<b>335.42</b>	<b>6.27</b>	<b>0.019</b>	<b>0.07</b>	<b>0.41</b>	+
			<b>OM</b>	<b>324.13</b>	<b>13.68</b>	<b>0.001</b>	<b>0.13</b>	<b>0.54</b>	+
			<b>C/N</b>	<b>320.66</b>	<b>5.11</b>	<b>0.03</b>	<b>0.04</b>	<b>0.58</b>	+
			Others	319.91	2.45	0.129	0.02	0.60	+
	Year	NH <sub>4</sub> <sup>+</sup>	<b>pH</b>	<b>613.36</b>	<b>11.91</b>	<b>0.001</b>	<b>0.19</b>	<b>0.19</b>	-
			Others	613.1	2.18	0.15	0.03	0.22	+
			C/N	612.39	2.57	0.12	0.04	0.26	-
	Year	PO <sub>4</sub> <sup>3-</sup>	<i>Marenzelleria</i> density	312.25	1.98	0.16	0.03	0.29	-
			<b>Others</b>	<b>315.44</b>	<b>7.31</b>	<b>0.01</b>	<b>0.12</b>	<b>0.12</b>	-
			<b>Salinity</b>	<b>309.61</b>	<b>7.97</b>	<b>0.008</b>	<b>0.12</b>	<b>0.24</b>	+
	Year	Si <sup>4+</sup>	<b>pH</b>	<b>307.11</b>	<b>4.34</b>	<b>0.04</b>	<b>0.06</b>	<b>0.30</b>	+
			<b>pH</b>	<b>644.63</b>	<b>4.41</b>	<b>0.04</b>	<b>0.10</b>	<b>0.10</b>	-
	Year	Combined	<b>Salinity</b>	<b>737.19</b>	<b>6.25</b>	<b>0.006</b>	<b>0.11</b>	<b>0.11</b>	+
			<b>Temp</b>	<b>732.41</b>	<b>6.82</b>	<b>0.004</b>	<b>0.11</b>	<b>0.21</b>	+
			<i>Marenzelleria</i> density	731.94	2.34	0.10	0.04	0.25	-
	High	Combined	<b>Salinity</b>	<b>407.83</b>	<b>6.38</b>	<b>0.004</b>	<b>0.19</b>	<b>0.19</b>	+
			Temp	407.46	2.21	0.13	0.06	0.25	+
			<b><i>Marenzelleria</i> density</b>	<b>405.13</b>	<b>4.04</b>	<b>0.04</b>	<b>0.10</b>	<b>0.35</b>	+
			<b>OM</b>	<b>404.09</b>	<b>2.66</b>	<b>0.09</b>	<b>0.06</b>	<b>0.41</b>	-

	Low	Combined	Temp	363.82	0.79	0.41	0.035	0.035	-
			Salinity	362.22	3.40	0.06	0.13	0.17	-
			C/N	364.14	0.07	0.95	0.003	0.17	-
			Macoma density	366.05	0.07	0.95	0.003	0.17	+
			Marenzelleria density	363.66	3.61	0.07	0.14	0.31	-
			pH	358.47	5.94	0.01	0.18	0.49	-
	Spring	Combined	Macoma density	144.22	3.66	0.07	0.31	0.31	-
			Marenzelleria density	136.56	11.40	0.007	0.43	0.74	-
			Others	133.32	3.83	0.04	0.10	0.84	+
IV (33m)	Year	NO <sub>x</sub>	Salinity	371.55	15.93	0.001	0.27	0.27	+
			Marenzelleria density	370.55	2.90	0.09	0.05	0.31	-
		NH <sub>4</sub> <sup>+</sup>	Temp	598.76	6.79	0.01	0.13	0.13	-
		PO <sub>4</sub> <sup>3-</sup>	Temp	450.99	12.44	0.001	0.22	0.22	-
			C/N	449.62	3.27	0.08	0.06	0.28	-
			Others	447.74	3.70	0.06	0.06	0.33	-
		Si <sup>4+</sup>	Others	560.31	9.96	0.06	0.10	0.10	+
	Year	Combined	OM	516.53	18.55	0.000	0.30	0.30	-
			Marenzelleria density	512.44	6.08	0.02	0.09	0.38	-
			Temp	509.56	4.70	0.04	0.06	0.45	-
			C/N	504.78	6.51	0.01	0.08	0.25	-
			Others	504.13	2.37	0.13	0.03	0.55	-
			Macoma density	503.86	1.98	0.17	0.02	0.57	+
	High	Combined	Temp	236.41	7.90	0.01	0.26	0.26	-
			OM	231.22	7.34	0.01	0.19	0.45	+
	Low	Combined	Temp	343.87	3.15	0.10	0.14	0.14	+
			Marenzelleria density	343.78	1.89	0.19	0.08	0.21	-
			C/N	339.69	5.74	0.02	0.19	0.40	+
	Spring	Combined	Marenzelleria density	85.08	6.59	0.04	0.62	0.62	-
			Macoma density	77.99	10.65	0.05	0.29	0.92	-
b) exp	Oct 2014	NO <sub>x</sub>	Bioirrigation	194.60	3.88	0.06	0.17	0.17	-
			Hediste biomass	193.23	3.13	0.10	0.12	0.29	+
		NH <sub>4</sub> <sup>+</sup>	M. arctica density	245.07	20.95	0.00	0.52	0.52	-
			Cerastoderma biomass	-11.03	8.07	0.01	0.30	0.30	+
		PO <sub>4</sub> <sup>3-</sup>							
			D <sub>b</sub> <sup>N</sup>	-11.76	2.50	0.13	0.09	0.38	-
			M. neg+vir density	-13.53	3.34	0.09	0.10	0.48	+

	Si <sup>4+</sup>	<b><i>Cerastoderma</i> biomass</b>	<b>297.19</b>	<b>12.55</b>	<b>0.00</b>	<b>0.40</b>	<b>0.40</b>	-
		<i>M. neg+vir</i> density	296.44	2.51	0.13	0.07	0.47	-
		MPD	296.22	1.90	0.18	0.05	0.52	-

c) BT param	Selected predictors	AIC	Pseudo-F	P	Prop.	Cum-R <sup>2</sup>	Corr.
MPD	<b><i>Hediste</i> biomass</b>	<b>-8.12</b>	<b>10.12</b>	<b>0.01</b>	<b>0.35</b>	<b>0.35</b>	+
	<b><i>Macoma</i> biomass</b>	<b>-10.67</b>	<b>4.35</b>	<b>0.06</b>	<b>0.13</b>	<b>0.47</b>	+
	<b><i>Marenzelleria</i> biomass</b>	<b>-12.46</b>	<b>3.36</b>	<b>0.08</b>	<b>0.09</b>	<b>0.56</b>	+
	<b><i>Marenzelleria</i> biomass</b>	<b>-106.09</b>	<b>12.14</b>	<b>0.002</b>	<b>0.39</b>	<b>0.39</b>	+
D <sub>b</sub> N	<i>Marenzelleria</i> biomass	-20.68	2.92	0.11	0.13	0.13	+
	<i>Hediste</i> biomass	-21.50	2.59	0.12	0.11	0.24	+
	<i>Macoma</i> biomass	-22.13	2.27	0.15	0.09	0.33	+
BI	<b><i>Marenzelleria</i> biomass</b>	<b>144.07</b>	<b>14.57</b>	<b>0.00</b>	<b>0.43</b>	<b>0.43</b>	+
	<b><i>M. arctica</i> density</b>	<b>141.86</b>	<b>4.00</b>	<b>0.06</b>	<b>0.10</b>	<b>0.54</b>	+
	<i>Cerastoderma</i> biomass	140.97	2.51	0.13	0.06	0.60	+

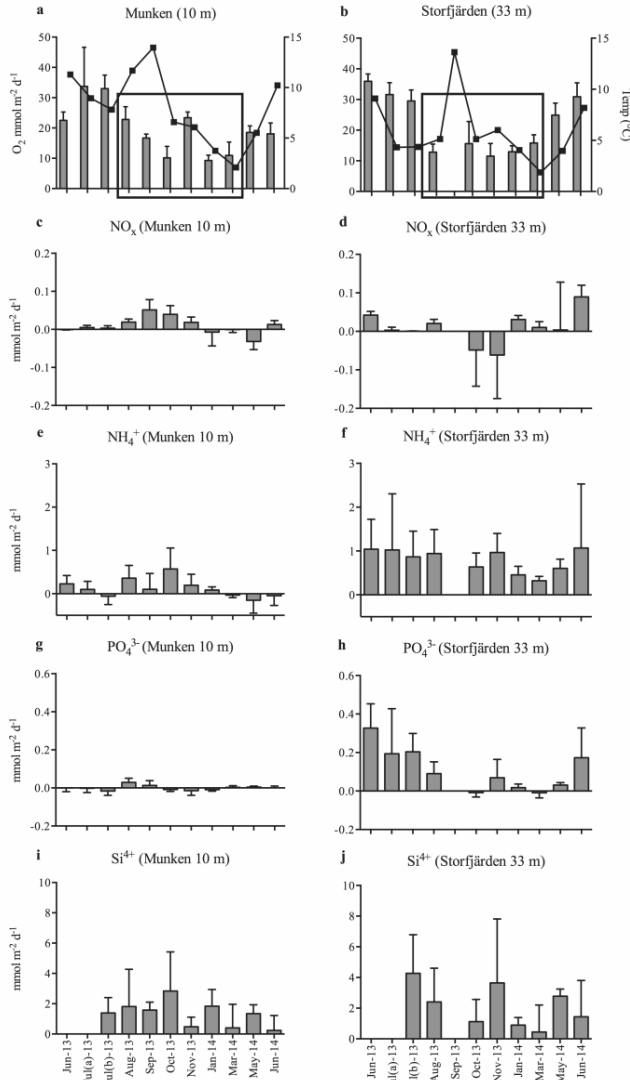
## 5.5 SEASONAL DRIVERS OF ECOSYSTEM FUNCTIONS

The marked seasonal variation in the abiotic conditions at temperate and high latitudes is reflected in the community dynamics (Paper II & III; Coma et al. 2000, Degen et al. 2015), and translated into the seasonal changes in the solute fluxes (Fig. 4 & 5 this thesis). Oxygen consumption, which can be used as a proxy for the macrofaunal and microbial activities in the sediment (Glud 2008), had a clear seasonal pattern at both study sites indicating a period of higher activity of sediment processes from June to August at the deeper (IV, 33 m), and from June to September at the shallower (II, 10 m) site (Fig. 5 a-b this thesis). The patterns in solute fluxes over the year reflected the pattern in oxygen consumption, environmental factors and faunal densities (Paper III; Fig. 4 & 5 this thesis). Organic matter and temperature act as triggers of degradation processes, and activity of the macrofauna and microbial communities (Moodley et al. 2005, Braeckman et al. 2010). Over the year the organic matter quantity and quality, temperature, and the density of *M. arctica* were important factors affecting nutrient cycling at the deeper site, whereas salinity and temperature have the largest effect at the

shallower site (Table 1a this thesis). The environmental factors thus seem to be more important in determining the functioning of the shallower site in general. However, the relative importance of abiotic and biotic drivers changed seasonally with the macrofauna, and especially *Marenzelleria* spp., having a very large effect during spring when the spring bloom provides food to the benthos (Heiskanen & Tallberg 1999) after a long winter similarly to deep-sea communities (Moodley et al. 2005).

The experimental results demonstrated the mechanisms by which *Marenzelleria* spp. affects solute fluxes, and revealed differences in the outcome depending on species identity and density of *Marenzelleria* spp. and of other organisms, similarly to the results of Karlson et al. (2016). Both abiotic and biotic factors vary in space and time, which has implications for the ecosystem structure and functioning and contributes to the context-dependency of the outcome of BEF studies (e.g. Jones et al. 2011, Perkins et al. 2015). The density-dependence of the bioturbation parameters implies differences in the fluxes affected by these over the season following changes in the densities of *Marenzelleria* spp. and other fauna (Paper II). For example the enhanced bioirrigation by increasing densities of *M. arctia* and increasing biomass of *Marenzelleria* spp. implies that when the densities and biomasses are higher in spring and summer, the importance of *Marenzelleria* spp. on the cycling of solutes is higher, as was also demonstrated by their high importance during spring (Paper III). Following the arrival of *Marenzelleria* spp. some sites have even gained three species with differing seasonal population dynamics (Paper II). The higher stability of populations of *Marenzelleria* spp. at the deepest, muddy site and the shallow sandy site could be important for their functioning (Stachowicz et al. 2002). In general, the variation and the magnitude of the solute fluxes was greater at the deeper site (Fig. 5), which was relatively organic-rich and had more stable populations of large *Macoma balthica* and *M. arctia*, and had less variation in the abiotic factors than the shallower site. The largest differences in fluxes between the sites was observed for ammonium and phosphate, with several times higher fluxes at the deeper site, indicative of the higher organic content and higher remineralization

rates at the deeper site. Thus even though both abiotic and biotic factors vary more at the shallower site, the seasonal differences in the fluxes are smaller than at the deeper site.



**Figure 5.** Seasonal oxygen (a-b),  $NO_x$  (c-d), ammonium (e-f), phosphate (g-h) and silicate (i-j) fluxes at the study sites Munken, II (left panels), and Storfjärden, IV (right panels). The line in (a-b) shows the bottom-water temperature at each sampling occasion. The box indicates the division of the year into periods of high and low oxygen consumption used as the two seasons in the statistical analyses. Figure modified from Paper III.

The differences between the sites are small with regards to most of the abiotic factors affecting nutrient cycling, however the magnitude and direction of the individual fluxes differ indicating that the same key species have variable effects on the same process depending on the environmental setting and on the solute in question (Fig. 5 & 6 this thesis). Figure 5 illustrates the seasonal changes in the solute fluxes at the two study sites whereas in figure 6 the correlation of the fauna and environmental factors on  $\text{NO}_x$  and  $\text{PO}_4^{3-}$  fluxes from Paper III over the year is illustrated in multivariate space. The negative effect of *Marenzelleria* spp. density on phosphate fluxes possibly through sediment oxygenation and binding with iron oxyhydroxides was only observed at the deeper site during summer, when the oxygen conditions deteriorate due to the formation of the summer thermocline preventing the mixing of the water column (Fig. 6). At the shallower, well-oxygenated site the correlation between phosphate flux and *Marenzelleria* spp. density was always positive. The association between *Marenzelleria* spp. and phosphate fluxes under the natural abiotic and biotic conditions was overall low, which was also observed in the experiment (Table 1b, Fig. 6). Furthermore, the indirect effect of *Marenzelleria* spp. through bioturbation on phosphate fluxes was small due to the non-significant effect of *Marenzelleria* spp. on the bioturbation parameter, the biodiffusion coefficient, associated with the phosphate fluxes. Higher phosphate fluxes have been measured in hypoxic than in normoxic areas in the study area and *Marenzelleria* spp. has been found to be an important predictor of nutrient cycling in general also under hypoxic conditions (Gammal et al. 2017). Thus it can be concluded that the effect of the polychaetes on phosphate binding can be seasonally important in areas with low bottom-water oxygen concentrations, but less so under normoxic conditions (Paper III, IV; Bonaglia et al. 2013).

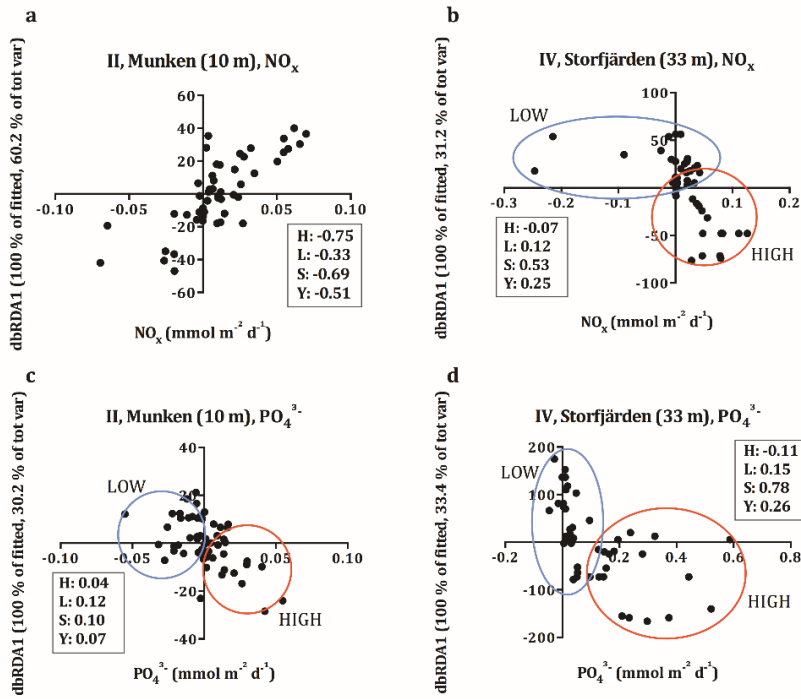


Figure 6. Fluxes of  $\text{NO}_x$  (a-b) and  $\text{PO}_4^{3-}$  (c-d) at Munken, II (left panel) and Storfjärden, IV (right panel) over the year expressed as a function of the Euclidean distance between the samples in the fitted model from Table 1a. See Table 1a for the selected predictors in the fitted models. The box shows the correlation between *Marenzelleria* spp. density and the solute during the period of high oxygen consumption (H), the period of low oxygen consumption (L), spring (S), and over the entire year (Y). The red circles indicate the period of high oxygen consumption and blue circles indicate the period of low oxygen consumption in the analyses. Figure based on results from Paper III.

Especially at the shallower site *Marenzelleria* spp. was a very important predictor of the inorganic nitrogen fluxes during spring and summer. Bioirrigation by macrofauna enhances nitrogen cycling by increasing the oxygen concentrations in the porewater thus increasing the area for the nitrification-denitrification processes. The contribution of *Marenzelleria* spp. to denitrification has previously been found to be low (Hietanen et al. 2007). Comparing the fluxes with abundances, it seems likely the negative correlation of *Marenzelleria* spp. with the  $\text{NO}_x$  would be caused by the peaking juvenile abundances in May together with a clear influx of  $\text{NO}_x$ . The enhancement of bioirrigation following increasing abundances of



*Marenzelleria* spp. identified in the experiment (Paper IV) is a likely explanation of the strong association between *Marenzelleria* spp. and the NO<sub>x</sub> fluxes. The enhancement of ammonium fluxes by *M. arctia* density can also indirectly affect the NO<sub>x</sub> fluxes by affecting the availability of ammonium for the nitrification process (Jäntti et al. 2011, Kristensen et al. 2011a). The results of this thesis imply that the effect of the invader is generally more important for nitrogen cycling than for phosphorus cycling in non-hypoxic areas but this effect is both site- and density-dependent (Table 1). Due to the organic matter availability coinciding with high abundances of *Marenzelleria* spp. at the sites where recruitment of *M. neglecta* and *M. viridis* occurs during spring, the importance of the genus for the nitrogen cycling could be seasonally very high.

The experimental results show that *Marenzelleria* spp. has the potential to significantly affect the fluxes of all solutes, but the observational results on the other hand imply that abiotic factors may override this effect (Godbold & Solan 2009), for example temperature and organic content at the deeper site during the period of high oxygen consumption. The experimental results also show that the outcome depends on the other species present in the community and their interactions with *Marenzelleria*, implying that the abiotic and biotic conditions shaping the community composition and species abundances in this way have indirect effects on ecosystem functioning. For example the possible intra- and interspecific competition, as well as the association with the organic matter availability observed for certain cohorts (Paper II) can affect the strength of the density-dependence of the BEF-relationships and the invader effects. Assessing the seasonal drivers of solute fluxes at the two study sites, it also becomes clear that the relative importance of abiotic versus biotic drivers varies spatially: the shallower site seems in general more driven by changes in the environmental factors, whereas the deeper site is more driven by the biological factors and only indirectly by the environmental factors. The biotic-driven deeper site shows greater variation in ecosystem functioning.

## **5.6 IMPLICATIONS OF THE EFFECTS OF THE SUCCESSFUL INVASION OF *MARENZELLERIA* SPP. ON THE BALTIC SEA ECOSYSTEM**

Paper I demonstrated that the three *Marenzelleria* species have spread to the entire Baltic Sea and become a dominant member of the benthic communities, particularly in deeper areas. This warranted a further investigation of their ecology and ecological impact, in this case on secondary production, and nutrient cycling. They have increased the species richness in the Baltic Sea, and in some, deeper, areas, also the functional richness (this thesis, Hewitt et al. 2016). They have contributed to enhanced secondary production especially in areas where all three species co-occur, and the association of their density with the organic content implies an enhancement of organic matter processing especially when densities peak during recruitment in spring and late summer/fall (Paper III; Jäntti et al. 2011, Karlson et al. 2011). This can be seen primarily as a positive effect, as the effective use of organic matter prevents accumulation, and the energy is incorporated into secondary production. A part of the secondary production is also transferred to other trophic levels, e.g. through *Hediste* predation. These interspecific interactions still need further study.

The Baltic Sea has been affected by eutrophication since the 1950's and even though some areas show signs of improvement, most are still classified as having a poor or bad environmental status, including the study area Gulf of Finland/northern Baltic Sea (Andersen et al. 2017). Nitrogen and phosphorus are key elements in eutrophication, and controlling the discharges of these nutrients into the Baltic Sea is the core of management actions (HELCOM 2013). In addition to anthropogenic inputs of these nutrients, the environmental conditions in the Baltic Sea promote eutrophication e.g. due to the naturally occurring stratification of the water column that prevents mixing of bottom and surface waters, which lead to a build-up of nutrients and hypoxia in the deep waters especially where the organic matter production is high (Conley et al. 2009). The increase in the hypoxic area has led to a decrease in the phosphate storing capacity of the sediment (Carstensen et al. 2014). Phosphate release especially benefits harmful cyanobacteria capable of fixing

their own nitrogen (Vahtera et al. 2007). Toxic cyanobacterial blooms are not only a nuisance to people but also e.g. to livestock grazing at the water's edge. The toxins can also accumulate in mussels and fish (Sipiä et al. 2001), possibly impairing their condition and making them poor-quality food for higher consumers. The potential density-dependent positive impact of *Marenzelleria* spp. on phosphorus binding, especially in disturbed areas, or during periodic hypoxia, can thus also benefit organisms on higher trophic levels by reducing cyanobacterial blooms. At shallower sites not affected by hypoxia the effect of *Marenzelleria* on phosphorus retention is negligible, instead they contribute to phosphorus release by enhancing organic matter remineralization. This effect, however, also depends on the other species present in the community and as indicated by the experimental results. This highlights that species and their effects should not be considered in separation from the surrounding community, whether non-native or native, and experiments should take this into consideration. The presence of the cockle *C. glaucum*, for example, was the most important predictor of phosphate fluxes (Table 1), but in the absence of other macrofauna its effect has been found to be less important (Mermillod-Blondin et al. 2004). The implications of both the observational and the experimental results of the direct and indirect (through bioirrigation) effects on nitrogen cycling also differ between sites. This can be due to the species identity: at the deeper site only *M. arctica* was found (Papers II and III) with a positive density-dependent direct and indirect effect on the nitrogen fluxes (Paper IV), whereas at the shallower site *M. neglecta* and *M. viridis* dominated, with possible indirect effects through bioirrigation, but no demonstrated direct effects (Paper IV). However, the strong negative correlations between *Marenzelleria* spp. and nitrogen fluxes at the shallower site during spring and summer indicated a seasonally high contribution for nitrification-denitrification processes when organic matter is available (Jäntti et al. 2011).

With ongoing climate change, temperatures are expected to increase and salinity decrease in the Baltic Sea (Stocker et al. 2013). This can induce shifts in species distributions and/or in their abundances, possibly affecting the strength of inter- and intraspecific

interactions. The experimental results presented in this thesis imply density-dependent effects of the non-native *Marenzelleria* spp. on nutrient cycling with varying outcomes depending on the composition of the surrounding communities and the variation in the abiotic factors. At different depths, the density-dependent, seasonally variable effects of *Marenzelleria* spp. demonstrated in this thesis might thus change in the future due to shifts in abiotic drivers directly affecting e.g. *Marenzelleria* spp. population dynamics, or indirectly affecting the densities of other species in the community. This could induce shifts in ecosystem functions and therefore in the magnitude and direction of the processes. The potential of *Marenzelleria* spp. to affect all the studied bioturbation parameters suggests they could be able to some degree compensate the loss of functions if other species in the community were to decrease in abundance or disappear. This, and the positive effects on phosphate binding has important implications especially in deeper, hypoxia-affected areas, where *Marenzelleria* spp./*M. arctia* often is the dominating taxon (Paper I, Paper IV).

## 6 CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH

Even in a well-known system such as the Baltic Sea, where the environment is thought to be well explored, this thesis was able to demonstrate previously unknown patterns and mechanisms. The overall aim of this thesis was to assess the ecology and ecosystem effects of the invasive polychaete *Marenzelleria* spp. in the northern Baltic Sea. The species complex was found to occur in the entire Baltic Sea, with the three species showing differing habitat preferences and population dynamics. They have increased species and functional richness in the communities, and their biomass production, especially high at sites where all three species recruit, can benefit other trophic levels through consumption. Due to variation in both environmental factors, as well as populations of *Marenzelleria* spp. and other macrofauna over the year, their relative importance for nutrient cycling varied across seasons. The non-native *Marenzelleria* spp. were capable of enhancing all bioturbation parameters to a certain degree, whereas the native fauna could not. It is important to bear in mind that these effects also depend on the species identity and density of *Marenzelleria* spp. This implies spatial and temporal differences in ecosystem functioning additionally depending on the variation in community composition and the environment. Notably, the polychaetes have the potential to enhance phosphorus binding in especially deeper, seasonally hypoxic areas, where they often are numerically dominant, but not necessarily in shallower, normoxic areas. They also have an important effect on nitrogen cycling through their bioirrigation. Though nutrient cycling can be enhanced by *Marenzelleria* spp., which can be seen primarily as a positive impact from the ecological point of view, their bioturbation can have effects on other processes that can have negative impacts. For example Hedman et al. (2011) and Granberg et al. (2008) have demonstrated release of contaminants from the sediments following *Marenzelleria* spp. bioturbation. More studies in this regard are needed, but in the end, if an overall assessment of the threat or opportunities the species

complex poses is required, it will require (subjective) judgement of which of the processes affected by the “invader” is more important.

The results highlight the need to consider the whole community and not species in isolation when studying the effects of invasive, or other, species on ecosystem functioning since their effects in isolation can be very different than inside an interaction network. The observational results also highlight the need for more long-term studies of BEF relationships to reveal the possible seasonal changes in their strength preferably combined with experimental results for increased understanding of the mechanisms behind certain functions. The variation in abiotic factors that drive the population dynamics and trigger the activity of macrofauna and microbes need to be well known in order to be able to predict the possible dynamics in the biotic environment. Following changes in the abiotic environment the role of native and non-native species alike and their effect on ecosystem functioning can change in the future. The implications e.g. of the role of *Marezzelleria* spp. on phosphorus and nitrogen cycling, and how this might affect other trophic levels also emphasizes the necessity of including multiple trophic levels in the BEF studies (Brose & Hillebrand 2016).

BEF studies have traditionally focused on species loss rather than species gain due to the primary interest in species extinctions driving the interest in these relationships. However, biological invasions, as also demonstrated by this study, often lead to species gain and changes in densities. Therefore, more studies on density-dependence of BEF-relationships with varying densities of organisms with differing trait composition are needed as well as experiments conducted in as natural an environment as possible with regards to biotic community composition for a realistic understanding of the species-specific effects within the natural environment. These will also benefit the studies on invasive species often undergoing an increase in population densities, which hence can change their ecological impact.

With regards to invasion biology the results of this thesis imply: know your species and know your environment (Bohlen et al. 2004, Petchey & Gaston 2006, Davis et al. 2011, Davis & Chew 2017). In this regard, non-native species do not differ from native species in

any way. Because species eradication in marine systems are most often not possible, preventing new invasions continues to be important, since we cannot accurately predict their impact in advance. The context-dependency of the effects of invasive species has been demonstrated in several studies, and therefore the management and conservation efforts should focus on evidence of the functions and not on the origin of species (Davis et al. 2011). Results from several BEF studies suggest that the anthropogenic impact on ecosystems will greatly modify the patterns and strength of biotic interactions and BEF relationships (Eisenhauer et al. 2016). Rather than focusing the debate on this, we should focus on what is causing the changes in the abiotic environment allowing species to enter and establish in new areas in the first place, i.e. focus on the cause and not just the consequence. As Davis et al. (2011) pointed out, non-native species have a very bad reputation among the public, managers and even scientists. The use of provocative terminology in the field has promoted the negativity towards non-native species or invaders, often without a clear definition of the terms being given (Davis et al. 2011, Simberloff et al. 2013, Russell & Blackburn 2017). The point of view of ecologists and that of conservationists or socio-economists might be different considering the impact of non-native species, but would not an ecosystem functioning more effectively from an ecologist's point of view also be something to strive for from an economist's or conservationist's point of view? Also, nativeness does not guarantee a positive effect on the ecosystem in a changing environment, nor does non-nativeness guarantee a negative effect. In the end, though, arguing over whether or not to judge a species by its origin blurs the ultimate, primary cause of how the debate even started: human-caused changes in the environment, degradation of habitats, and increased globalization (Briggs 2017). These effects do not care if the species in the community are native or not, they will act upon the variation present and the outcome will be dependent on the species identity, traits, the environment, and their respective interactions.

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